Mimetic Associations in Natural Populations of Tropical Papilionid Butterflies. (Lepidoptera: Papilionidae)

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Abstract: A long-term capture-mark-recapture program was conducted on *Parides* (Papilioninae) butterflies (*Parides arcas mycale*, *Parides arcas mylotes*, *Parides childrenae childrenae*, and *Parides erithalion sadyattes*) visiting the flowers of two widely-separated *Hamelia patens* (Rubiaceae) trees in Costa Rican lowland tropical rain forest. Adult populations, composed predominantly of males, were present at these two feeding sites for more than 12 successive months. These small populations were characterized by long-lived males not subject to heavy predation, and "residential" in terms of their local movements in the jungle. Such low-turnover populations persisted at feeding sites over long periods. This persistence, in addition to similar diurnal activity periods among species accounted for an effective Müllerian mimetic association. Females were highly vagile, presumably due to searching behavior for oviposition sites, and thus irregularly appeared at low frequency at the regular feeding sites of males. The localized distributions of males at their feeding sites could function primarily for initiation of courtship behavior in the jungle, favoring effective female dispersal after successful mating. Females may act as models in mimetic associations with other species (*Papilio anchisiades ideaus*, *Papilio* sp., and *Heliconius doris*) seen in the jungle, but like females of *Parides*, adults of these species were also irregular, infrequent visitors at these feeding sites and exhibited high vagility.

INTRODUCTION

This paper discusses a 14 month study on the size and structure of adult populations for tropical papilionid butterflies belonging to the genus *Parides* that comprise Müllerian mimicry complexes in a Costa Rican lowland tropical rain forest. Interest centers upon temporal trends in population size for each species in two mimicry complexes, changes in age-structure in populations of each species, relative survivorship of adults of each species from predation by birds, and upon diurnal patterns of activity for the different species. The species studied are:

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Parides arcas mylotes Bates (hereafter referred to as *Parides mylotes* to avoid confusion with the following subspecies), *Parides arcas mycale* Goodwin & Salvin (hereafter referred to as *Parides mycale* to avoid confusion with *Parides mylotes*), *Parides childrenae childrenae* Gray, and *Parides erithalion sadyattes* Druce. Based on geographical information given in Seitz (1924), it is held that the subspecies *mycale* of *Parides arcas,* known especially from Panama, represents a transitional form between the Mexican *mylotes* subspecies and the South American *arriphus* form of this species. There are also other South American subspecies (*agathokles* and *antheas*) of *Parides arcas.* For *Parides childrenae,* there is the Central American form, *childrenae,* in addition to the South American form, *oedippus.* The *sadyattes* form of *Parides erithalion* is recorded from Costa Rica and Panama, and there are several South American forms of this species (*zeuxis, cauca,* etc.). Within-species variation in *Parides* may be due to unstable evolutionary processes that represent recent splits of species into several subspecies and perhaps has little bearing on mimicry. Variations seen in local populations are insufficient to make the species appear "polymorphic" to potential predators, since all forms within species appear similar. Directional selection on the one hand attributing greater fitness to individuals possessing an extreme size, and stabilizing selection on the other hand, in which individuals in the modal size classes have greater fitness, are two forces that could account for observed size distributions which are independent of age effects in an animal population. Different sympatric species, even those closely related, may be expected to exhibit varying amounts of such selective effects due to differences in genetic make-up and slight differences in actual selective pressures. Sex-related color variation among males within a population could be a result of local selective forces that are counteracted with gene flow, mechanisms that account for the existence of geographical forms (clines) in butterfly populations (Lucas 1969). The variation encountered within *Parides* represents different selective pressures than those for other polymorphic tropical butterflies and serving as models in mimicry complexes (e.g., Turner and Crane 1962).

A quantitative study on mimicry complexes in the tropics not dealing with papilionids, (Young 1971), discusses the mimetic interactions between two other tropical papilionids, *Battus polydamus polydamus* L. and *Battus belus varus* Kollar in Costa Rica. At least one of these species, *Battus polydamus,* feeds during larval life upon *Aristolochia* (Aristolochiaceae) and although foodplant records are not yet available for *Battus belus,* it is likely that they also feed on *Aristolochia* (Young in prep.). Species of at least two other genera in the Papilioninae, *Parides* and *Troides,* are also known to feed on *Aristolochia,* and due to the high alkaloid content of the leaves of these vines (Willaman and Schubert 1961), the butterflies of these and other genera of the tribe Troidini have been called the "pharmacophagus" swallowtails (Seitz 1924) or "Aristolochia swallowtails." Of the eight genera comprising the Troidini which are represented both in the New and Old World tropics (except Africa) (Seitz 1924), most species feed on the Aristolochiaceae but with individual species also recorded from distantly related plant groups such as Rutaceae, Menispermaceae, Nepenthaceae, and Piperaceae (Ehrlich and Raven 1964). The Aristolochiaceae comprise the major foodplants of these butterflies and the vines have their greatest distribution and diversification within the Old and New World tropics (Good 1947; Pfeifer 1966). At least three of the species of *Parides* studied here oviposited on various species of *Aristolochia.* It is assumed that all of the species discussed in this paper are distasteful and could act as effective models against avian predation; furthermore, their co-occurrence on a regular basis at flowers in a tropical rain forest constitutes an effective Müllerian mimicry association. This assumption is based on laboratory data showing that one species of *Parides* (*Parides neophilus parianus*) is very distasteful to Blue Jays (Brower and Brower 1964), and the larvae of this species feed on *Aristolochia* sp. in Trinidad. While there is no comparable data available on mimetic associations of *Parides neophilus* in natural populations, it is assumed that such a species would be avoided by birds as a preferred food source.

While this study focused upon mimetic interactions among species of *Parides* butterflies at feeding sites, additional observations were made on mimetic interactions with other species, namely: *Papilio anchisiades idaeus*, F., an unidentified *Papilio*, and *Heliconius doris transiens* Stgr. (Heliconiinae). Both sexes of these species appear similar to female *Parides* and both sexes of *Parides erithalion* may interact mimetically with *Papilio anchisiades.* There probably exists little mimetic interaction of any *Parides* species with these butterflies, while effective mimetic relationships among males are maintained within localized *Parides* complexes.

OBSERVATIONS

During the period September–November 1968, various species of *Parides* butterflies, of the "red and black" variety, were regular visitors at the red flowers of a small tree, *Hamelia patens* (Rubiaceae) which is widely and commonly scattered along the edges of primary-growth tropical rain forest in the lowlands of northeastern Costa Rica. Finca La Selva, a 1300-acre tract of forest owned by The Organization for Tropical Studies, Inc., and situated on the confluence of two rivers, the Rio Sarapiqui and the Rio Puerto Viejo, was the study area. It is located about 2 miles south of the village of Puerto Viejo de Sarapiqui (10° 26′ N, 83°59′ W; 89 m elev.) in the Heredia Province of Costa Rica. The general vegetation of this region is "premontane tropical wet forest" (Holdridge 1967), represented a climatic region characterized by a long wet season and short, but highly variable (in intensity and duration) dry season ("verano") between January and March each year. Although the dry season is characterized by a reduction in rainfall in this region of Costa Rica, the "1969 dry season" was unusually dry, while the "1970 dry season" (not shown) was similar to the 10-year average. (Fig. 1). The 1969 dry season was characterized by less rain and was 2.5 months longer. It was assumed that the rainfall pattern (measured) at Puerto Viejo was similar to that at Finca La Selva (hereafter referred to as "La Selva"), without major departures. Only fragmentary rainfall data (Allen M. Young, personal communication) were available from La Selva, but when inspected, these agreed with trends seen in the monitored Puerto Viejo rainfall.

Hamelia patens is a tropical tree species that blooms continually at La Selva (Gordon Frankie, personal communications), despite the dry season. Thus, it represents a consistently available source of nutrients for various kinds of insects that forage at its flowers for nectar. Individual trees, 10–15 feet high, bloom throughout the year and facilitate the study of butterfly activity. Insects may be readily observed at close range. It is easy to capture (net) several species of butterflies visiting *Hamelia* flowers, mark them with a light-weight enamel-base fast-drying paint ("Flo-Paque"), and release them within a few minutes after capture. At La Selva, various species of *Parides* butterflies fed almost exclusively at *Hamelia* flowers at this level in the forest. At a different locality in northeastern Costa Rica, near San Miguel de Sarapiqui (also premontane tropical wet forest), at least one species of *Parides* (*Parides mycale*) is a frequent visitor at flowers of *Stachytarpheta jamaicensis* (Verbenaceae) (Allen M. Young, personal observations), but at La Selva, barring gross sampling error, neither this species nor others forage at flowers other than *Hamelia* at the understory level in the forest. Such foraging is consistent throughout the year, although there are seasonal changes in abundance of adults of each species of *Parides* at *Hamelia*.

During early January 1969, two widely-separated and heavily-blooming *Hamelia patens* trees (of comparable size) were selected as study sites for a long-term capture-mark-resight program involving all species and all individuals per species of *Parides* butterflies seen visiting the flowers on these trees. The study basically consisted of observing on several days each month the relative numbers of each species of *Parides* seen at each of these two "feeding sites" at La Selva. The first *Hamelia* tree used for these observations (Study Site 1) was located in dense, old second-growth vegetation about 30 feet from the north bank of the Quebrada El Sura, and about 40 feet from the left side of the "El Sura Trail." It was a 3-minute walk from the field station facility. The vegetation surrounding this blooming *Hamelia patens* tree was extremely dense, and consisted of a large stand of *Urera elata* (Urticaceve) plants 5–8 feet tall covered with various young vines, including *Aristolochia* spp., a known foodplant for *Parides* (Seitz 1924). From the trail leading to the stream, this study site was almost invisible. The second *Hamelia* tree (Study Site 2) was located about 500 meters west of Study Site 1 and about 20 feet from the west side of the Quebrada

Table 1. Numbers of individuals of the butterfly species in a *Parides* mimicry complex visiting regularly at flowers of the tree, *Hamelia patens* ("Study Site 1") on Finca La Selva, Heredia Province, Costa Rica, 14 January 1969–19 March 1970 (14 months).

		Numbers of marked and unmarked (parentheses) butterflies seen within 4–6 hours on a given day				
Dates	No. Samples	*Parides mycale*	*Parides mylotes*	*Parides childrenae*	*Papilio anchisiades*	*Papilio* sp.
14–27 Jan '69	6	8 (0)	8 (0)	2 (0)	0 (4)	1 (0)
10–18 Feb '69	5	8 (0)	8 (0)	2 (2)	0 (2)	1 (0)
12–20 Mar '69	7	6 (0)	8 (0)	4 (0)	1 (5)	1 (0)
3–11 Apr '69	8	6 (2)	7 (1)	4 (0)	0 (2)	0 (0)
16–22 May '69	8	8 (2)	8 (0)	4 (2)	0 (3)	0 (0)
10–19 June '69	8	10 (0)	8 (0)	3 (1)	0 (0)	0 (0)
5–13 July '69	7	10 (3)	6 (0)	4 (1)	0 (2)	1 (0)
18–26 Aug '69	6	7 (2)	6 (3)	4 (0)	1 (1)	1 (2)
7–15 Sept '69	7	9 (1)	8 (1)	4 (0)	2 (0)	2 (0)
11–19 Oct '69	7	10 (0)	9 (0)	4 (2)	0 (4)	1 (0)
15–23 Nov '69	7	10 (3)	7 (0)	6 (0)	0 (1)	1 (0)
18–25 Jan '70	6	8 (0)	7 (0)	6 (0)	0 (1)	0 (0)
10–14 Feb '70	5	8 (0)	7 (0)	6 (2)	0 (2)	0 (0)
11–12 Mar '70	2	7 (1)	7 (1)	8 (0)	0 (0)	0 (0)

Leonel. It was situated close to primary-growth rain forest where a small cacao (*Theobroma cacao*) grove filled a thin strip of land bordering the Rio Puerto Viejo (north of Study Site 2). Large patches of young second-growth vegetation were intermingled with this cacao grove. The two study sites, separated by several hundred meters of jungle, were visited regularly by various species of *Parides* butterflies. On the ventral surface of the hindwings a large dot of paint was applied. Sex differences and wing condition were recorded by coded markings. From these records it was possible to estimate monthly trends in adult numbers within each species at each feeding site, and to observe trends in adult survivorship, both from mortality associated with old age and from predation. It was assumed that old and worn individuals that "disappeared" from a population had died from old age and were not killed by birds or had not migrated from the area. Such assumptions were justified by concomittant trends in residentiality of individuals observed, and from the low frequency of beak-marks seen on adults. Observations were made on activity of *Parides* at each *Hamelia* tree on several days each month, usually between 8:30 A.M. and 3:00 P.M. (C.S.T.). Occasionally the observation period extended to 6:00 P.M. in order to assess diurnal activity patterns in each species with respect to foraging. The assumption was also made that each of the two blooming *Hamelia* trees provided the major nutrient source for the *Parides* butterflies seen visiting them regularly. This assumption appears justified since individuals (especially males) of each species were residential and did not seek other food sources in the habitat. Usually, a given feeding site was observed for 3–6 successive days each month at La Selva, although there were a few times when this schedule was modified.

Table 2. Numbers of individuals of the butterfly species in a *Parides* mimicry complex visiting regularly at flowers of the tree, *Hamelia patens* ("Study Site 2")[a] on Finca La Selva, Heredia Province, Costa Rica, 3 March 1969–20 April 1970 (12 months).

		Numbers of marked and unmarked (parentheses) butterflies seen within 4–6 hours on a given day				
Dates	No. Samples	*Parides mycale*	*Parides mylotes*	*Parides childrenae*	*Papilio anchisiades*	*Papilio* sp.
3–9 Mar '69	5	6 (0)	5 (1)	3 (0)	1 (0)	0 (0)
20–24 Apr '69	4	6 (0)	5 (0)	3 (0)	1 (3)	0 (0)
25–29 May '69	4	5 (2)	4 (2)	2 (0)	0 (0)	0 (2)
17–23 June '69	5	7 (0)	6 (1)	0 (0)	0 (3)	0 (1)
14–19 July '69	4	7 (1)	7 (0)	0 (4)	1 (2)	1 (0)
17–23 Sept '69	5	8 (2)	7 (0)	4 (0)	0 (0)	1 (0)
7–10 Oct '69	2	10 (0)	7 (3)	3 (1)	0 (0)	0 (1)
11–14 Nov '69	3	9 (0)	10 (1)	4 (1)	1 (2)	0 (0)
26–30 Jan '70	4	9 (2)	11 (0)	5 (0)	0 (0)	2 (0)
16–21 Feb '70	4	11 (0)	10 (0)	5 (0)	0 (0)	0 (0)
21–25 Mar '70	4	10 (0)	9 (1)	5 (0)	0 (1)	0 (0)
28–30 Apr '70	2	9 (0)	10 (0)	3 (1)	0 (0)	0 (2)

[a] This study site consisted of a small group of blooming *Hamelia patens* trees located about ½ mile from Study Site 1, and in the same type of tropical second-growth vegetation.

Observations were made at ground level using binoculars, although binoculars were not always necessary due to the closeness with which one may approach these feeding butterflies. Unmarked individuals that appeared at each site after the study was begun were captured, marked according to species, sex and individual number, and released at the same spot. Other species that appeared to resemble *Parides* were also netted, marked and released using a different coding system. The marking technique did not appear to interfere with the butterflies normal activity and apparently marked individuals were not injured. Observations initiated during January 1969 were continued on a monthly basis until April 1970. Observations at Study Site 2 were initiated in March 1969. The period of observation at each study site was 14 months for Study Site 1 and 12 months for Study Site 2 with no data obtained during the month of December for both sites, and the month of August 1969 for Study Site 2. On several occasions each month, less regular observations were made on courtship behavior, oviposition, and larval behavior.

POPULATION STRUCTURES AND MIMETIC INTERACTIONS

From January 1969 through March 1970, adults of *Parides mycale*, *Parides mylotes*, and *Parides childrenae* were regular foragers at the flowers of both *Hamelia* trees, and monthly numbers of adults of each of these species are summarized in Tables 1 and 2. Despite the continuous flowering of *Hamelia* throughout the dry seasons in 1969 and 1970 at La Selva adult numbers of all species of *Parides* dwindled during the early part of these periods (January, February). There was no recruitment of teneral adults to the foraging male populations and the

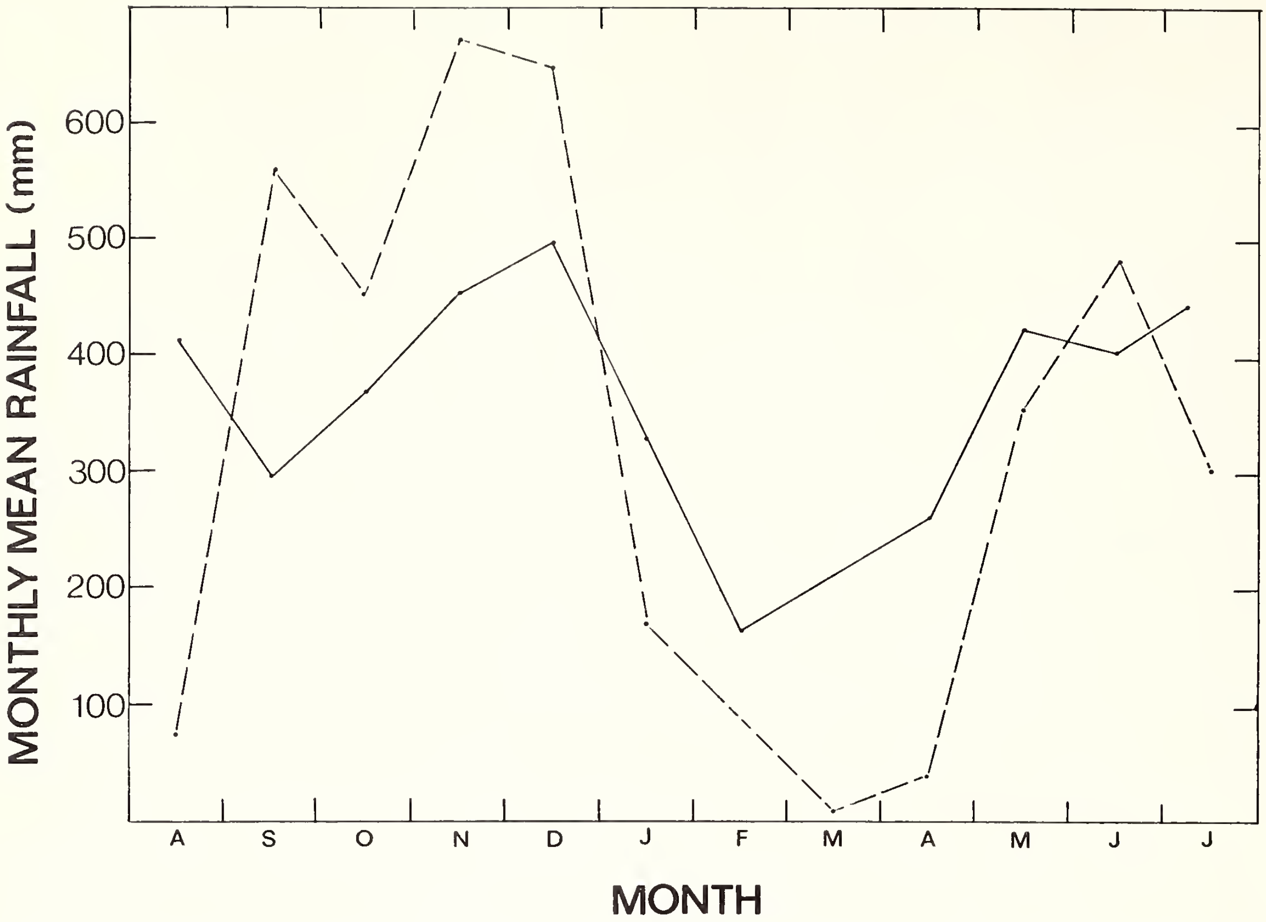

FIG. 1. Seasonal pattern of rainfall at Puerto Viejo, Heredia province, Costa Rica. Solid line–ten year monthly averages; broken line–1969 rainfall pattern. Data courtesy of Servicio Meteorologico de Costa Rica.

precise reasons for these declines are not known. There may be seasonal effects on larval development in which larvae develop more slowly or enter a diapause period until the end of the dry season. Such larval behavior has recently been observed for *Morpho peleides* (Morphinae) in El Salvador, in which fourth-instar larvae become quiescent for about 30 days during the dry season, and complete development (there are 5 instars) only with the onset of the wet season (Alberto Muyshondt, personal communications). Whether or not similar behavior exists for other species of tropical butterflies is not known at the present time. Data concerning monthly occurrences of *Parides erithalion* are excluded here since adult numbers were extremely low (1–3 individuals seen at a *Hamelia* tree on an irregular, sporadic basis) and there were usually several days each month when no adults were seen at each feeding site. The remaining species of *Parides* occur regularly at both feeding sites during the study periods (Tables 1 and 2), and one species, *Parides childrenae,* was consistently lowest in adult numbers each month. While admittedly we are dealing with low population densities for all species, *Parides childrenae* was consistently the least abundant species in the two mimicry complexes in question. Being dissimilar in appearance from both subspecies of *Parides arcas,* selective

Table 3. Sex ratios of butterfly species in a *Parides* mimicry complex visiting regularly at flowers of the tree, *Hamelia patens*, Study Site 1, in a lowland tropical wet forest in northeastern Costa Rica (Finca La Selva, Heredia Province), January 1969–March 1970.

		Numbers of Marked Individuals by Sex								
		Parides mycale			*Parides mylotes*			*Parides childrenae*		
Months	N[a]	♀♀	♂♂	T	♀♀	♂♂	T	♀♀	♂♂	T
Jan '69	6	2	6	8	3	5	8	0	2	2
Feb.	5	2	7	9	3	5	8	1	3	4
Mar	7	1	5	6	3	5	8	1	3	4
Apr	8	3	5	8	2	5	7	1	3	4
May	6	2	8	10	2	6	8	1	5	6
June	8	2	8	10	2	6	8	0	4	4
July	7	3	9	12	1	5	6	0	5	5
Aug	6	2	7	9	1	5	6	0	4	4
Sept	7	2	8	10	2	7	9	0	4	4
Oct	7	2	8	10	2	7	9	2	4	6
Nov	7	3	10	13	1	6	7	2	4	6
Jan '70	6	2	7	9	2	7	9	2	4	6
Feb	5	1	8	9	3	7	10	3	5	8
Mar	5	3	5	8	4	4	8	2	6	8

[a] N is the number of days of observation each month when butterfly activity was highest at this nectar source.

factors may operate to keep the numbers of *Parides childrenae* lower than *Parides arcas* in order to maintain an effective Müllerian mimetic interaction. These species are undoubtedly distasteful to birds and the less abundant any departure from the more frequent forms in the complex, the more likely the dissimilar form will escape attempted predatory attacks. At low population sizes in tropical butterflies, attempted predatory attacks by birds could result in local extinctions of species, even species involved in Müllerian mimicry complexes. A "successful" attack in small populations characterized by individuals of low vagility, could lead to local extinction. It has been demonstrated that small populations can be subjected to random extinction (Wilson and MacArthur 1967), and superimposed biotic effects such as predation could hasten this.

While adult populations of *Parides* at the two feeding sites were small, they consisted predominantly of males (tables 3 and 4). Females appeared on a less regular basis than the males. Sometimes for 2–3 successive days marked females of any species (but especially *Parides childrenae*) did not visit a feeding site. There was an apparent number of "residential" females that visited at each feeding site, and presumably these individuals were part of nearby breeding populations. Based on observations made in the immediate vicinity of feeding sites (usually within 200 feet), it was apparent that marked females wander considerable distances away from feeding sites, presumably in search of suitable oviposition sites. At Study Site 1, scattered patches of

TABLE 4. Sex ratio of butterfly species in a *Parides* mimicry complex visiting regularly at flowers of the tree, *Hamelia patens*, Study Site 2, in a lowland tropical wet forest in northeastern Costa Rica (Finca La Selva, Heredia Province) March 1969–April 1970.

		Numbers of Marked Individuals by Sex								
		Parides mycale			*Parides mylotes*			*Parides childrenae*		
Months	N[a]	♀♀	♂♂	T	♀♀	♂♂	T	♀♀	♂♂	T
Mar '69	5	2	4	6	1	5	6	0	3	3
Apr	4	2	4	6	1	4	5	0	3	3
May	4	1	5	6	1	5	6	0	2	2
June	5	2	5	7	2	5	7	0	0	0
July	4	2	5	7	2	5	7	1	3	4
Sept	5	3	5	8	2	5	7	1	3	4
Oct	2	3	7	10	3	7	10	2	2	4
Nov	3	2	7	10	3	8	11	2	3	5
Jan '70	4	2	9	11	3	8	11	2	3	5
Feb	4	2	9	11	3	7	10	2	3	5
Mar	4	2	8	10	2	7	9	2	3	5
Apr	4	2	7	9	2	8	10	1	3	4

[a] N is the number of days of observation each month when butterfly activity was highest ("sunniest days") at this nectar source.

Aristolochia spp. were present and females of *Parides mycale* and *Parides mylotes* were seen occasionally resting on vegetation associated with these vines. Sex ratios at feeding sites, sex ratios of adults emerging from egg clusters, and degree of residentiality of males versus females, suggest that female *Parides* were more vagile than males. Related to the apparent irregular occurrence of females of these species of *Parides* at the two feeding sites studied were the concomitant irregular visitations of potential mimics of these butterflies. *Papilio anchisiades* and *Papilio* sp. were infrequent visitors at these feeding sites, and resightings of previously-marked individuals were low (tables 1–2). An unrelated form, *Heliconius doris* is also seen at widely scattered intervals (days of observation) each month, and marked individuals were rarely resighted, even within 5 days after marking. Such observations on potential mimics of female *Parides*, and the irregular visitation patterns of female *Parides* at feeding sites, suggests that mimetic interactions at feeding sites may be restricted to Müllerian associations only among males of various species of *Parides*. The male associations among *Parides* butterflies appeared most stable at feeding sites, in terms of the regularity (daily and monthly) of individual male visitations at flowers. Little is known about time for learning by would-be vertebrate predators in order to associate distastefulness with color in natural populations of tropical butterflies and therefore little can be said about the effectiveness of mimicry involving *Parides* females at feeding sites where males are regular foragers. It was the male component of each species-population that was maintained at feeding sites over long

TABLE 5. Diurnal pattern of courtship[a], egg-laying, and feeding in sympatric, local populations of *Parides mycale*, *Parides mylotes*, and *Parides childrenae*, at Finca La Selva, a lowland tropical wet forest site in northeastern Costa Rica.

	Mean Number of Adults[b] Seen Hourly for Different Categories of Activities[c]								
	Parides mycale			*Parides mylotes*			*Parides childrenae*		
Time (C.S.T.)	Feeding	Courtship	Oviposition	Feeding	Courtship	Oviposition	Feeding	Courtship	Oviposition
A.M.									
8:00–9:00	1	0	0	0	0	0	0	0	0
9:00–10:00	3	0	0	3	0	0	1	0	0
10:00–11:00	9	7	0	8	8	0	4	0	0
11:00–12:00	9	10	0	10	11	0	4	6	0
P.M.									
12:00–1:00	5	6	0	8	7	4	5	4	0
1:00–2:00	7	0	10	5	1	9	3	2	5
2:00–3:00	6	0	7	2	0	6	2	0	8
3:00–4:00	2	0	9	2	0	8	0	0	4
4:00–5:00	1	0	0	0	0	0	0	0	0
5:00–6:00	0	0	0	0	0	0	0	0	0

[a] Defined here as "directed, aerial pursuits of females by males in vegetation near feeding site"—see text for elaboration; given are the numbers of such pursuits witnessed.

[b] Data combined for the 2 study sites, with hourly means calculated over entire study period (using March 1969–March 1970 period).

one feeding site. Several species of male *Parides* may be present at a specific feeding site on a given day, and the temporal persistence of such interactions periods of time. It appears that much of the irregularity of foraging by these individuals at *Hamelia* was due to flying activity associated with oviposition (searching for oviposition sites). Female *Parides* and mimics such as *Papilio anchisiades*, *Papilio* sp., and *Heliconius doris* moved around in the forest far more than male *Parides*, as judged from the marking program, and effective mimetic associations among such individuals may not be established at any among species over long periods of time may provide the basis for an effective Müllerian mimicry complex at the feeding site. Males of *Parides mylotes, Parides mycale* and *Parides childrenae* were active at feeding sites during the same hours on sunny days at La Selva (table 5), and females of all three species were seen ovipositing during the afternoon hours. The few observations available on tandem pairs indicate that courtship occurs for all three species at the same times during the day (table 5). Cross-subspecies copulations have not been observed for *Parides mycale* and *Parides mylotes.* The common activity period for males of these species in regard to foraging at *Hamelia* flowers would serve to reinforce mimetic association among these species. Rothschild (1964) points out that selection should favor similar feeding periods for species involved in Müllerian mimicry complexes. Selection should favor similar courtship and oviposition periods in these species, since

TABLE 6. Numbers of adult *Parides*[a] bearing evidence of bird attack (beak-marks and wing damage) in mimicry complexes visting regularly at flowers of two *Hamelia patens* trees (Study Sites 1 and 2) at Finca La Selva, Heredia Province, Costa Rica. Data combined for the two sites.

	Parides mycale		*Parides mylotes*		*Parides childrenae*	
Months	Total	Damaged	Total	Damaged	Total	Damaged
Jan[a]	8	1	8	0	2	0
Feb	9	1	8	0	4	0
Mar	12	2	14	2	7	0
Apr	14	2	13	2	7	0
May	17	3	14	1	8	2
June	17	2	15	2	4	1
July	21	4	13	4	9	0
Aug	9	1	9	0	4	0
Sept	20	2	16	3	8	1
Oct	19	0	19	1	10	2
Nov	22	3	18	0	12	1
Jan	19	1	20	2	11	3
Feb	20	0	20	1	13	1
Mar	18	2	18	3	13	0
Apr	9	0	10	1	4	0

[a] Combined data for both sites, except Jan, Feb, and August 1969, and April 1970, when data from only one feeding site is available.

such activities determine, in part, the local survivorship of the species at low population numbers in the forest.

Whether or not effective Müllerian mimicry is actually operating between *Parides* species at feeding sites or merely each species displays a warning coloration that, devoid of mimetic effects, can induce a "fright" response in

TABLE 7. Age-distribution in an adult male population of *Parides mycale*, based on examinations of marked individuals over several successive months at a feeding site (No. 1), flowers of a *Hamelia patens* tree in a lowland tropical wet forest (Finca La Selva, Heredia Province) in northeastern Costa Rica.

		Relative Numbers in Various Age-classes				
Months	N	"Tenerals" (1–12 days)	"Young" (10–25 days)	"Middle Age" (1–3 mo.)	"Old" (3–5 mo.)	"Very Old" (5–7 mo.)
Jan	3	0	0	3	4	1
Feb	4	0	0	3	3	2
Mar	4	0	0	1	5	0
Apr	5	1	1	1	3	2
May	5	2	2	1	3	2
June	4	0	3	2	2	3
July	4	3	1	3	3	3
Aug	4	2	3	3	1	0
Sept	5	1	5	1	2	1
Oct	5	0	2	4	2	2
Nov	4	3	0	5	3	2
Jan	4	0	1	6	1	0
Feb	4	0	0	5	3	0
Mar	3	1	0	3	3	1

Table 8. Age-distribution in an adult male population of *Parides mylotes*, based on examinations of marked individuals over several successive months at a feeding site (No. 1), flowers of a *Hamelia patens* tree in a lowland tropical wet forest (Finca La Selva, Heredia Province) in northeastern Costa Rica.

Months	N	Relative Numbers in Various Age-classes				
		"Tenerals" (1–12 days)	"Young" (10–25 days)	"Middle Age" (1–3 mo.)	"Old" (3–5 mo.)	"Very Old" (5–7 mo.)
Jan	3	0	0	5	2	1
Feb	4	0	0	3	4	1
Mar	4	0	0	3	2	3
Apr	5	1	0	2	3	2
May	5	0	1	2	3	2
June	4	0	0	1	4	3
July	4	0	0	1	4	1
Aug	4	3	0	0	5	1
Sept	5	1	3	0	5	0
Oct	5	0	2	2	3	2
Nov	4	0	1	2	4	0
Jan	4	0	0	1	5	1
Feb	4	0	0	0	4	3
Mar	3	1	0	0	3	4

would-be avian predators (Coppinger 1969) was not be discernible in this study, although it was apparent that individual survivorship from such mortality is high (table 6). Adults, presumably damaged by bird attacks, were retrieved from populations at La Selva. The incidence of such nonseasonal mortality within a localized "group" of males visiting a feeding site is very low. Adults "disappear" from a feeding site when they become "old" or "very old" (tables 7–9), and presumably this represents deaths due

Table 9. Age-distribution in an adult male population of *Parides childrenae*, based on examinations of marked individuals over several successive months at a feeding site (No. 1), flowers of a *Hamelia patens* tree, in a lowland tropical wet forest (Finca La Selva, Heredia Province) in northeastern Costa Rica.

Months	N	Relative Numbers in Various Age-classes			
		"Tenerals" (1–20 days)	"Young" (14–40 days)	"Middle Age" (2–4 months)	"Old" (4–7 months)
Jan	3	0	0	2	0
Feb	4	2	0	2	0
Mar	4	0	2	0	2
Apr	5	0	0	2	2
May	5	2	0	1	3
June	4	1	2	1	0
July	4	1	1	3	0
Aug	4	0	1	2	1
Sept	5	0	0	2	2
Oct	5	2	0	1	3
Nov	4	0	2	0	4
Jan	4	0	1	1	4
Feb	4	2	0	2	4
Mar	3	0	0	4	4

to old age rather than predation. Younger adult males (tables 7–9) seldom disappeared from populations associated regularly with *Hamelia* flowers. Based on changes wing condition, estimation of the age-structure of a male *Parides* population associated with a given feeding site can be established. although more precise bracketing of age classes was unfeasible under field conditions. It is possible to conclude (tables 7–9) that individual males (and presumably females) are long-lived (a maximum of 6–7 months) obviously avoiding predation. Adult population turnover was generally low at feeding sites (tables 1–2) and most unmarked males seen during the study periods were "fresh" in wing condition, apparently recently emerged from pupae. No major emigration of older adults to these feeding sites from other places in the forest was observed and presumably the adult male populations regularly associated with different feeding sites (*Hamelia* trees) represented a component localized breeding population of high residentiality. Adult male populations at La Selva were small, localized, and had low rates of turnover. Individual male *Parides* movements possessed low vagility in terms of their daily activities.

Such population "cohesiveness" in male *Parides* feeding associations at *Hamelia* may in part be accounted for in terms of butterfly behavior at these sites in the jungle. From observations on marked males, virtually every one of these individuals within species perched regularly close to the actual *Hamelia* tree. By careful searching the perching sites for all three species of males in the second-growth vegetation associated with each feeding site were located. Day-to-day perching sites for males when not feeding were variable, yet each male on a given day repeatedly returned to the same plant for perching. Resting males intercepted passing males and females of any *Parides* species, but the significance of this behavior is not clear at this time. Homing ability of individual males was well developed. Aggressive assaults exclusively within species have not been observed. Males flew off with the passing of either sex for any species in similar flight behavior and appeared to "chase" the passing butterfly without contacting it. Such pursuit movements were typically terminated within several seconds by return of the "challenger" either to the perching site or to feeding at *Hamelia* flowers.

Little is known about larval mortality and survivorship through the pupal stage in natural populations. Such mortality will have to be estimated for observed local adult (male) densities at feeding sites. Lack of comparable numbers of females at feeding sites was probably related to searching behavior of oviposition sites. The observed aberrant sex ratios at feeding sites seen in this study cannot be explained in terms of density-related dispersal mechanisms in which females respond to increasing population densities by migrating to new habitats for reproduction (Shapiro 1970). At low population densities, presumably fertilized females disperse from centers of male activity (feeding sites and immediate vicinity), cruising through the jungle in search of suitable *Aristolochia* vines for oviposition.

Dispersal behavior by females may be induced by behavior of males at feeding sites. Preliminary observations suggest that males will chase females in the immediate vicinity of feeding sites and while such "pursuit" behavior is not density-related (Shapiro 1970), it may cause females to leave the area. Selection favors the dispersal of females away from places of high male concentration to ensure oviposition with minimal loss of energy and time in post-mating interactions with males. In a few instances in which males were observed chasing females of their own species, the chase led away from the feeding site. Perhaps the initial phases of courtship behavior in these butterflies take place at feeding sites although copulating pairs were not observed at feeding sites. It is also possible that adult males are territorial at feeding sites, although further, detailed observations on male-male interactions within species must be carried out to determine and characterize such behavior.

From the observations summarized here on relative abundances of adult males, it is apparent that the feeding behavior among different *Parides* at common foraging sites, is specialized and accounts, in part, for the localized distributions of adult *Parides* in lowland tropical rain forests. The apparent lack of seasonal changes in this behavior for these butterflies represents a "specialization of niche" that is usually characterized for organisms associated with the non-seasonal wet tropics (e.g., Slobodkin 1970).

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